Cumulative cultural evolution within evolving population structures

Authors: Maxime Derex[1]* & Alex Mesoudi[2]

[1] Institute for Advanced Study in Toulouse, UMR 5314, Centre National de la Recherche Scientifique, Toulouse 31015, France.

[2] Human Behaviour and Cultural Evolution Group, Department of Biosciences, University of Exeter, Penryn TR10 9FE, United Kingdom.

Correspondence to: maxime.derex@iast.fr (M. Derex)

Keywords: cultural evolution; cumulative culture; demography; group problem-solving; population size; population structure; social learning

Abstract

Our species possesses the peculiar ability to accumulate cultural innovations over multiple generations, a phenomenon termed cumulative cultural evolution (CCE). Recent years have seen a proliferation of empirical and theoretical work exploring the interplay between demography and CCE. This has generated intense discussion about whether demographic models can help explain historical patterns of cultural changes. Here, we synthesise empirical and theoretical studies from multiple fields to highlight how both population size and structure shape the pool of cultural information that individuals can build upon to innovate, present the potential pathways through which humans' unique social structure might promote CCE, and discuss whether humans' social networks might partly result from selection pressures linked to our extensive reliance on culturally accumulated knowledge.

Problem-solving in populations over multiple generations

A central feature of our species is our unprecedented capacity to develop sophisticated cultural practices that have allowed us to colonize and permanently occupy environments for which we are poorly suited genetically [1, 2]. This capacity can be viewed as a form of problem-solving by which humans have successfully solved complex ecological challenges. This form of problem solving, however, is peculiar in that it operates at the population level, rather than solely within individuals, and over multiple generations [2, 3]. Both traditional and more modern technologies have not been produced by a single individual but have emerged over centuries through incremental improvements resulting from the efforts of multiple generations of individuals. This process - known as **cumulative cultural evolution** (CCE) - is powered by our ability to selectively learn adaptive social information which results in the gradual accumulation of **innovations**, and can give rise to cultural traits (such as technologies) that are beyond individuals' inventive capacities [2-7].

Drawing predominantly on ideas from evolutionary theory, anthropologists, biologists and psychologists have developed a rigorous theoretical framework that applies the notion of descent with modification to material culture, and have investigated the role of population dynamics in the production, transmission and maintenance of cultural traits [8-10]. An influential finding of early theoretical models is that our social learning abilities interact with **demography** to affect CCE, and, more specifically, that the size of the population within which cultural information is shared strongly constrains CCE [11].

Recent years have seen a proliferation of empirical and theoretical work exploring the interplay of demography and CCE, and demographic factors are increasingly invoked to explain historical patterns of cultural changes [11-19]. While this research has advanced our understanding of the link between demography and CCE and opened up promising new avenues, it has also revealed a need to better articulate empirical research and theoretical models. Here we present the theory, discuss misconceptions, outline future challenges, and highlight new directions in research on demography and CCE.

Strength in numbers

Demography has long been considered a potential explanation for cultural changes documented in the archaeological record [20-22], but it is with the theoretical work of Shennan [23] and Henrich [11] that the idea gained prominence among evolutionary human scientists. The main idea behind demographic models of cultural evolution is that, given that CCE only operates when at least some information is transmitted socially between generations [24-26], the **effective population size** (which depends on both population size and interconnectedness) can buffer the risk of losing cultural information (see Box 1). In Henrich's seminal model [11], for instance, individuals belong to a population of constant size and possess a psychological propensity to learn from successful individuals. This propensity creates a selective force that promotes the transmission of beneficial cultural traits and outweighs the degrading effects of learning errors when populations are large enough (Figure 1). These results suggest that decreases in

effective population size (due to phenomena such as plagues, war or volcanic eruptions) might result in losses in individuals' level of skills (often proxied in the archaeological literature as the number of tools, or toolkit complexity) by constraining CCE. Several regional losses of cultural traits documented in the archaeological record, such as prehistoric Tasmania, have consequently been attributed to decreases in population size and connectedness [11, 19]. Conversely, the emergence of more complex cultural traits have been hypothesized to result from increases in population sizes and/or densities [13, 14].

Experimental tests of the relationship between population size and CCE

One approach that has been used to evaluate the plausibility of demographic models of CCE involves lab experiments. Typically, participants who are part of groups of different sizes are tasked to improve a piece of technology. To date, 5 experiments from 4 different research groups provide support for a positive effect of group size on cultural complexity [27-31] (but see [32, 33]). One study, for instance, exposed naïve participants in groups of 2, 4, 8 and 16 to demonstrations showing how to produce virtual arrowheads and fishing nets, and tracked the efficiency of those tools across time [27]. The larger the group, the less likely tools were to deteriorate, the more likely they were to improve, and the more likely a diversity of tool types were to be maintained. Using chains of participants and alternative tasks involving image-editing and knot-tying techniques, another study similarly showed that the deterioration of a technique is less likely (and its improvement more likely) in

larger groups [29]. Additionally, these experiments show that individuals use cues such as success to choose from whom they learn, lending plausibility to the assumption of Henrich's model that individuals selectively learn from successful **demonstrators**.

Importantly, some of these experiments relied on designs that only loosely reflect Henrich's initial assumptions (Box 2). Most, for instance, provide individuals with the opportunity to simultaneously learn and combine information from multiple demonstrators (a several-among-many design) [28-31] while Henrich's model assumes that individuals always select a *single* source of information from a larger pool of demonstrators. Some experiments that have relied on the former design, however, allowed participants to allocate their learning time strategically, which means that individuals' learning strategies might still, in practice, be consistent with Henrich's assumptions [29]. Yet mechanisms that are not part of Henrich's model, such as combining information from multiple demonstrators to generate new solutions, certainly did play a role in these experiments [29-31]. Due to this disconnect between experimental tests and theoretical models, it is not always clear whether experimental studies showing positive effects of demography offer genuine support for specific theoretical claims, nor whether purported failures to detect any effect of demography are valid challenges to theoretical models (see Box 2 for further discussion).

Real-world tests of the relationship between population size and CCE

A complementary and more direct approach to test the relationship between population size and CCE is to look for a correlation between toolkit size and population size using real-world ethnographic and archaeological data. Results with this approach have been mixed. Some studies support the hypothesis [13, 14, 34, 35], but others do not [36-39] (although [40] point out that some of these studies rely on the same datasets, and should not count as independent tests).

The difficulty with testing demographic models using real-world data is that human populations are typically embedded within extended networks of cultural exchange, making it difficult to gather meaningful estimates of population size. This constitutes a major obstacle for anthropologists and archaeologists because theoretical models explicitly link cultural complexity to the size of the population *that shares information* (i.e. the effective cultural population size) [11]. This implies that tests of demographic hypotheses should control for contact rates between inter-connected populations, which is typically challenging (but see [34]). Proponents of demographic hypotheses have therefore argued that studies which reported null results are invalid because they do not take contact rates into account and typically treat culturally connected groups as independent, culturally isolated populations [40] (see Box 3 for other mismatches between models and empirical tests).

Other studies have tested demographic effects where they may not be predicted to occur. One study, for instance, found no evidence that larger populations support more complex folk tales, with complexity operationalised as number of tale types, number of narrative motifs within tales, and number of component details within tales [41]. Yet folk tales are very different to the technology

144 that is the focus of most demographic models. Tools that are more efficient and
145 have higher payoffs are typically associated with an increasing number of
146 component elements [42], which means that they tend to be more complex.
147 However, if complexity is not associated with higher payoffs, then theoretical models
148 do not predict that population size should necessarily affect it. The function of
149 folktales, for instance, is to convey meaning. If similar meaning can be conveyed by
150 simpler folktales, we should not necessarily expect to observe the most complex
151 folktales in larger populations. The same line of reasoning applies to the evolution of
152 language, which functionally adapts to the needs of efficient communication [43].
153 Studies that have investigated the relationship between speaker population sizes
154 and phoneme inventory sizes [44-46] or rates of language change [47-49] have
155 yielded mixed results. However, because language also evolves to become more
156 learnable [50], we should not necessarily expect larger populations to produce more
157 new words nor have larger phoneme inventory size. Furthermore, folk tales and
158 other forms of expressive culture may serve as markers of group membership and
159 some models have suggested that smaller groups will have more exaggerated
160 markers [51]. This suggests that a clearer picture about the relationship between
161 demography and the evolution of expressive cultural traits might emerge by moving
162 away from arbitrarily chosen measures of complexity and by taking into account that
163 functional and symbolic cultural traits exhibit different evolutionary dynamics [52].

164 It is also worth stressing that, contrary to recent claims [53], no theoretical
165 work ever predicted that population size should *solely* determine the number of tools
166 (or any other measure of cultural complexity) found in human populations. Many

167 factors are expected to affect toolkit complexity in natural populations, including
168 mobility, subsistence practices and ecological factors. The risk hypothesis, for
169 instance, holds that populations living in harsh environments create more numerous
170 and specialised tools to mitigate the risk of resource failure due to stochastic
171 variation [36-39, 54, 55]. Importantly, the risk hypothesis and the population size
172 hypothesis differ in what they aim to explain [56]. The risk hypothesis explains what
173 determines the size and complexity of toolkits (i.e. what creates the need for cultural
174 complexity). The population size hypothesis is about the constraints imposed on
175 CCE. Claims that the absence of correlation between population size and toolkit
176 complexity disprove demographic models are based on misconceptions about
177 those models (see Box 3).

178 Inconclusive studies about the relationship between population size and CCE
179 have had the merit of stimulating new work and led to important refinements to early
180 theoretical work. Models with different assumptions have shown that the effects of
181 effective population size hold when more conservative or alternative assumptions
182 are considered (e.g. restricting potential demonstrators to a limited number of
183 acquaintances [57]; conformist transmission [58, 59] but see [60]; adding costs to
184 acquiring knowledge [61]; and alternative pathways to innovation [62]). However,
185 recent studies also suggest that the relationship between effective population size
186 and CCE can be mediated by numerous factors ([58, 62-66]), and that there are
187 numerous challenges in detecting demographic effects on CCE in real-world data
188 (see Box 3).

189 Despite these challenges, there is little doubt that changing the effective size

of a population will alter the cultural information available to subsequent generations of learners, which will most likely constrain what can be achieved by individuals. In this context, promising new work has started to investigate more broadly how constraints on information flow within populations can further promote or hinder the gradual accumulation of cultural innovations.

Beyond numbers: CCE in social networks

Human populations do not consist of a collection of isolated groups of varying sizes. Multiple groups are typically connected by migratory and trade activities, which results in wide, heterogenous social networks. The role of connectedness on CCE was already acknowledged in early theoretical models [11, 13]. A simulation model that explicitly implemented migratory activity among subdivided populations, for instance, showed that increasing the migration rate has a similar effect to increasing the size of an isolated population [13]. This is because increases in both population size and migratory activity increase the effective number of individuals available as demonstrators, and so reduce the risk of losing cultural information.

More recent work, however, has started to investigate in greater detail how the structure of the population impacts the accumulation of cultural information. Unlike early models, recent studies decouple the maintenance of existing traits and the production of new traits, more explicitly modelling the pathways that give rise to innovation [62, 67-69]. Recent models, for instance, assume that existing traits can not only be refined but also combined with other existing cultural traits. When **recombination** between existing traits is incorporated as a pathway towards

innovation, increases in population size and connectedness can have different effects on CCE [68, 69]. This is because, while increases in population size systematically benefit CCE by reducing the risk of cultural loss, increases in connectedness can *reduce* opportunities for innovation by homogenising cultural behaviours. This effect is illustrated by a recent lab experiment in which individuals could innovate by producing incremental changes within path-dependent technological trajectories (**refinement**) and by combining traits that have evolved along different trajectories (recombination) [67]. Results show that high levels of connectedness make individuals more likely to converge on similar solutions, which results in lower levels of cultural diversity and slower rates of innovation compared with less connected groups.

These results suggest that understanding the effect of demography on CCE requires us to consider not only how changes in connectedness affect the number of individuals available as demonstrators, but also how it shapes the cultural diversity to which individuals are exposed. When these two effects are considered simultaneously, models show that optimal rates of accumulation are reached for intermediate levels of connectedness [68, 69]. This is because low levels of connectedness increase the risk of cultural loss by decreasing access to demonstrators, while high levels of connectedness reduce opportunities to innovate by homogenising cultural behaviours. At intermediate levels of connectedness, groups can accumulate cultural information while remaining culturally distinct, which keeps fueling innovation.

These results have implications for CCE both at the macroscale and the

236 microscale. At the macroscale, human population have been historically fragmented
237 due to geographic barriers, conflicts and other factors, resulting in long-standing
238 culturally differentiated sub-populations. In this context, increased levels of
239 between-group connectedness are unlikely to homogenise cultural behaviours.
240 Nevertheless, recent models suggest that, because of new opportunities for
241 recombination, contacts between culturally differentiated groups should result in
242 rapid cultural changes whose magnitude far exceed what is predicted by models
243 that incorporate cultural loss alone [68]. This also suggests that population
244 structures that allow for contacts between culturally differentiated groups might act
245 as endogenous drivers of cultural change [67, 68], even though it should not be
246 assumed that populations will develop and maintain more complex cultural
247 repertoires without appropriate incentives to do so (Box 3).

248 Patterns of connectedness might also affect CCE at the microscale by
249 influencing individuals' exploration of the design space. Network and organization
250 scientists, for instance, have jointly shown that behaviours are more likely to become
251 homogeneous in well-connected than in partially-connected groups when learners
252 preferentially acquire information from the same demonstrator [70-72] (but see [73,
253 74]). Sociologists have similarly argued that behaviors tend to be more
254 homogeneous within groups than between groups and that individuals with ties to
255 otherwise unconnected groups have greater opportunities to develop new ideas
256 because they are exposed to a broader diversity of information [75].

257 These studies illustrate how patterns of connectedness impact the quantity
258 and diversity of information that individuals are exposed to and can draw on to

make inferences, which in turn can impact populations' abilities to develop and maintain cultural traits. The benefits of sparsely interconnected networks on CCE in natural populations, however, remain to be properly evaluated. Complex cultural traits are typically hard to learn and several experiments have stressed the importance of multiple demonstrations and multiple learning attempts in the acquisition of complex skills [27, 76]. This suggests that occasional contacts between different individuals/groups might not allow complex skills to spread properly. Additionally, network scientists have stressed the importance of the number of sources of exposures for the adoption of unproven new solutions [77]. Experiments typically provide participants with accurate information about alternative solutions, which allows them to confidently adopt the most rewarding ones. In noisy environments, however, interactions with multiple carriers might be critical for individuals to adopt alternative solutions [77] (see also [78] for an example of how the mean number of connections within a network affects the spread of cultural traits). Future research should test whether the optimal level of connectedness differs depending upon the characteristics of the cultural traits one is looking at. Dense networks, for instance, might be critical for the cultural evolution of hard to learn traits (for which transmission is the key bottleneck), while the cultural evolution of easy to learn traits whose efficiency can be readily assessed might be faster in sparsely connected networks.

Characterizing human social networks in the wild

The effects of population interconnectedness on CCE suggests that cultural

changes might be better understood by paying greater attention to the structure and evolution of human social networks. Mapping past, or even recent, social networks, however, is challenging. Archaeologists and geneticists are still struggling to infer past population sizes [15, 79, 80], let alone population structures [81]. In recent years, approaches relying on social network analyses have seen a rise among archaeologists, but many challenges have still to be solved before being able to distinguish spatio-temporal patterns in social interactions from noise in archaeological data [82-84].

Comparative and ethnographic studies, however, are already providing valuable information about human population structure. Comparisons between human hunter-gatherer societies and non-human primate societies, for instance, have shed light on what has been called the deep social structure of human societies [85]. Contrary to most non-human primate societies, which are composed of independent, single-group structures, human societies are federations of multifamily groups [85, 86]. This unique multigroup structure results in extensive networks of unrelated individuals that might be conducive to CCE [87]. Data on interactions between same-sex adults from two hunter-gatherer populations, for instance, reveal that individuals typically interact with more than 300 same-sex adults in a lifetime (although including opposite-sex adults and children results in estimates as high as 1000). In comparison, male chimpanzees are estimated to interact with only about 20 other males in a lifetime [87] (see also [88] for a discussion on the large-scale social networks of hunter-gatherer groups).

Other studies among hunter-gatherer populations have started to more finely

characterize hunter-gatherer networks. One study, for instance, used trackers to map in-camp networks in two hunter-gatherer populations and showed that individuals invest early in their childhood in a few close friends who bridge densely connected families [89]. These strong friendships increase the global efficiency of hunter-gatherer in-camp networks, which might facilitate the flow of social information (Figure 2). More recently, characterization of hunter-gatherer networks has been extended to between-camp interactions and has been used to simulate the accumulation of cultural innovations over real networks [90]. Results confirm that hunter-gatherers' social structures are made of multiple levels of clustering, and simulations suggest that this sparsely interconnected hierarchical network structure might accelerate CCE by allowing the coexistence of multiple cultural lineages and promoting the emergence of innovations (but see Box 4).

The few studies that have investigated networks in hunter-gatherers, however, have been limited to interview data and proximity measures [87, 89, 90]. Actual measurements of cultural transmission remain scarce, and the extent to which proximity networks accurately reflect transmission networks is currently unknown. Investigation of the co-occurrence of plant uses in dyads in one hunter-gatherer population, for instance, showed that not all knowledge is equally shared [91]. More specifically, results show that medicinal plants were mostly shared between spouses and kin, while plants that serve other functions were shared much more widely. This suggests that knowledge-sharing networks are content-specific and supports the idea that hunter-gatherer multi-level social structure enables culturally differentiated units to remain stable despite occasional co-residence [90]. This work also suggests

328 that both **structural barriers** (i.e. lack of contact between individuals) and
329 **behavioral barriers** (i.e. unwillingness to share cultural knowledge) have to be taken
330 into account to properly evaluate the effects of population structure on CCE. Indeed,
331 structural and behavioral barriers combine to result in an **effective population**
332 **structure** that ultimately determines opportunities for cultural transmission. Contact
333 between different ethnolinguistic groups, for instance, can potentially bring different
334 cultural traits together due to significant between-group cultural distance. However,
335 language barriers, endogamy, rivalry and other behavioural barriers such as in-group
336 conformity might limit opportunities for cultural exchange between those groups [92,
337 93].

338 These results suggest that our understanding of the relationship between
339 demography and CCE would benefit from a better understanding of how and why
340 individuals form social ties both within- and between-groups and the extent to which
341 different types of ties (such as kin-based, affine-based and friendship-based) are
342 conducive to cultural transmission. This will permit more realistic implementation of
343 cultural transmission into theoretical models. Indeed, while the combination of
344 vertical cultural transmission (i.e. learning from parents) and success-biased learning
345 is empirically supported and provides a useful first approximation of the dynamics of
346 social learning in groups [40], multiple factors are likely to affect opportunities for
347 social learning. Anthropological studies, for instance, have shown that social ties are
348 more likely to form between people who share similar traits (i.e. homophily [94, 95]).
349 Furthermore, understanding how individuals form social ties is an important avenue
350 for future research because the way individuals form ties ultimately feeds back into

351 the evolution of social networks (homophily, for instance, is known to introduce local
352 structure into networks [95, 96]).
353
354 ## How did human social networks get their shape?
355 Even if questions remain regarding the effects of specific network properties on
356 CCE, it seems clear that humans live within unusually large and uniquely structured
357 social networks. This raises questions about how and why humans have come to
358 form large networks of unrelated or weakly related individuals.
359 Recently, it has been argued that, because individuals from culturally
360 differentiated groups might have greatly benefited from increased between-group
361 interactions, selection might have acted at the individual level to affect individuals'
362 propensity to interact with out-group members [17]. This might have involved
363 changes in conscious behavioural choices (e.g. adjustments to out-group contacts
364 due to perceived immediate benefits) and/or unconscious influence on behaviour
365 (e.g. decreased fear of foreigners or tendency to disperse) [17]. Congruently, a
366 recent simulation model that investigated whether network structure itself can evolve
367 as a result of ecological pressures related to skill acquisition confirmed that
368 selection can impact individuals' propensity to form random ties (such as non kin
369 ties) [97]. Yet, it is not clear whether the acquisition of social information creates
370 sufficiently strong incentives for individuals to overcome rivalry and other
371 behavioural barriers that tend to reduce opportunities for cultural transmission
372 between unrelated individuals. Moreover, increasing contacts is only one part of the
373 problem, as many cultural traits are unlikely to be properly acquired without a

374 demonstrator's willingness to share information [98-100].

375 Another possible way by which selection might have promoted the
376 emergence of networks that are conducive to CCE is by acting on variation that
377 exists at the group level [17, 101]. Indeed, anthropologists have long stressed the
378 role of cultural institutions in promoting both information sharing and interactions
379 between non-kin [87, 101-103]. Among the Ache and Hadza, for instance, ritual
380 relationships, mediated by activities such as club fight rituals, have been shown to
381 promote inter-band interaction. Quantitative analyses have revealed that ritual
382 relationship is a more important predictor than kinship for different types of
383 interactions, including opportunities for cultural transmission (such as observing tool
384 making skills) [87]. Furthermore, anthropologists have stressed that certain groups
385 have cultural beliefs that connect envy and harm, which make successful individuals
386 more likely to hide information from other group members, thus inhibiting CCE
387 compared to other groups [101]. This suggests that groups that possess cultural
388 institutions that promote information sharing and/or mobility might have attained
389 higher cultural complexity and outcompeted groups with cultures less conducive to
390 CCE [17, 101]. It is also worth noting that the maintenance of large networks of
391 unrelated or weakly related individuals might have been further supported by the
392 emergence of cultural innovations such as kin naming systems and stylistic markers
393 of group identity that typically promote cooperative interactions between unrelated
394 individuals [103]. Kin naming systems, for instance, allow familial relationships to
395 extend to affine, distant kin and even non-kin [103] and might permit individuals to
396 maintain privileged relationships with large numbers of individuals without requiring

much cognitive effort nor physical cohabitation [104].

The question of whether humans' social structure might in part result from selection pressures linked to our extensive reliance on culturally accumulated knowledge will have to be carefully evaluated. Indeed, chimpanzees also live among nonrelatives [105] and humans' propensity to form ties with non-kin might be due to reasons unrelated to CCE and that just happened to be conducive to the accumulation of cultural innovations. Archeologists, for instance, noted that an incest avoidance rule would give rise to the same kind of sparsely connected networks that might benefit CCE [56]. Alternative determinants of outgroup contacts include resource distribution [56], reciprocal cooperative exchange [106] and coalition formation [107], among others. Specific predictions should be formulated and properly tested to disentangle the respective effects of these various mechanisms on network structure. The hypothesis that CCE directly shapes network structure by acting on conscious behavioural choices, for instance, would predict that individuals should flexibly reinforce or weaken their investment in non-kin ties depending on the usefulness of the information they provide.

Concluding remarks and future directions

The proliferation of work exploring the interplay of demography and CCE has recently led to many misconceptions due to loose interpretations of early theoretical models (Box 2 and 3). Empirical tests that operationalize models in ways that are consistent with theoretical assumptions provide support for the hypothesis that effective population size constrains CCE. However, testing these models using real-

world data remains difficult because multiple factors combine with demography to determine CCE and human populations are typically embedded within extended networks of cultural exchange. While these extended networks of contacts make it difficult to gather meaningful estimates of population size, recent research suggests that they might also affect CCE in ways that are not yet fully appreciated. Understanding how population structure affects CCE will require us to understand precisely how structural and behavioral barriers constrain information flow in natural populations (Box 4).

The effects of connectedness on the accumulation of cultural information raise many questions about the relationship between humans' unique social structure and CCE (see Outstanding Questions). Through the study of the nature and the emergence of non-kin ties, both within groups and between groups, as well as knowledge-sharing networks in natural populations, it will be possible to illuminate how humans have managed to accumulate cultural information in such an unprecedented way and determine whether our unique social structure results in part from selection pressures linked to our extensive reliance on culturally accumulated knowledge.

Box 1: Demographic models of cultural change

Cultural drift. Some of the earliest cultural evolution models adapted early 20th century models of genetic drift to the cultural case [8, 22, 23, 108]. Drift, whether genetic or cultural, is essentially sampling error. Drift models typically assume 'unbiased transmission' or 'random copying': each of N individuals within a finite and fixed-sized population possesses one of a set of discrete cultural traits. Each generation or timestep, individuals select another individual at random and acquire their cultural trait. This process results in the inevitable loss of trait variation. The speed with which traits are lost is dependent on N: smaller populations lose variation quicker. This is a highly simplistic model, but provides a useful base for exploring the effects of processes such as innovation and complex population structures such as island chains or bottlenecks on CCE, and has been used to explain archaeological assemblage diversity [22, 108].

The 'Tasmanian' model. Perhaps the most influential demographic model of cultural evolution was formulated by Henrich [11]. This model was inspired by the empirical case of prehistoric Tasmania, which apparently lost complex technological traits (e.g. bone tools, warm clothing) around 10-12kya when Tasmania was cut off from the Australian mainland, thus decreasing the effective population size [20]. The model incorporates more psychologically plausible processes than simple drift models. Each of N individuals possesses a value of culturally transmitted 'skill' (e.g. basket-making), represented by a continuous variable z. Each timestep, each individual attempts to learn the skill value z_h of the highest-skilled member of the

previous timestep, h (i.e. success biased transmission). Learning is imperfect, and affected by two kinds of processes. Learning error, determined by α, always results in worse skill than z_h. Another parameter, β, determines the extent of inferences, experiments, luck and other factors that on average make skill levels worse, but sometimes better, than z_h. Combining these, Henrich assumed that the skill of a naive individual is drawn from a Gumbel distribution (Figure 1). N interacts with the latter β term: the more individuals there are, the more likely one of those individuals is to exceed z_h, representing an increase in cumulative cultural knowledge/skill. If N is too small, then all learners will acquire values around the mode of the distribution, which is less than z_h, resulting in a decrease in cultural complexity. Subsequent empirical work has shown that this Gumbel distribution is a reasonable approximation of social learning dynamics [109] (but see [110] for a critique of this model).

Population structure and trait recombination. Subsequent models have extended the Tasmanian model to investigate in greater detail how the structure of the population impacts both the maintenance and the production of cultural traits. Stochastic simulations of the Tasmanian model with multiple sub-populations show that increasing the migration rate has a similar effect to increasing the size of an isolated population on CCE, because both increase variation within sub-populations and so reduce the risk of losing cultural information [13]. Recent studies have more explicitly modelled the pathways that give rise to innovation and revealed that the effect of migration can even be more pronounced when cultural traits can combine

to form innovations that are “greater than the sum of their parts” [68]. However, too frequent contact might not be beneficial to CCE because it prevents populations from remaining culturally distinct, and reduces opportunities to innovate [68, 69].

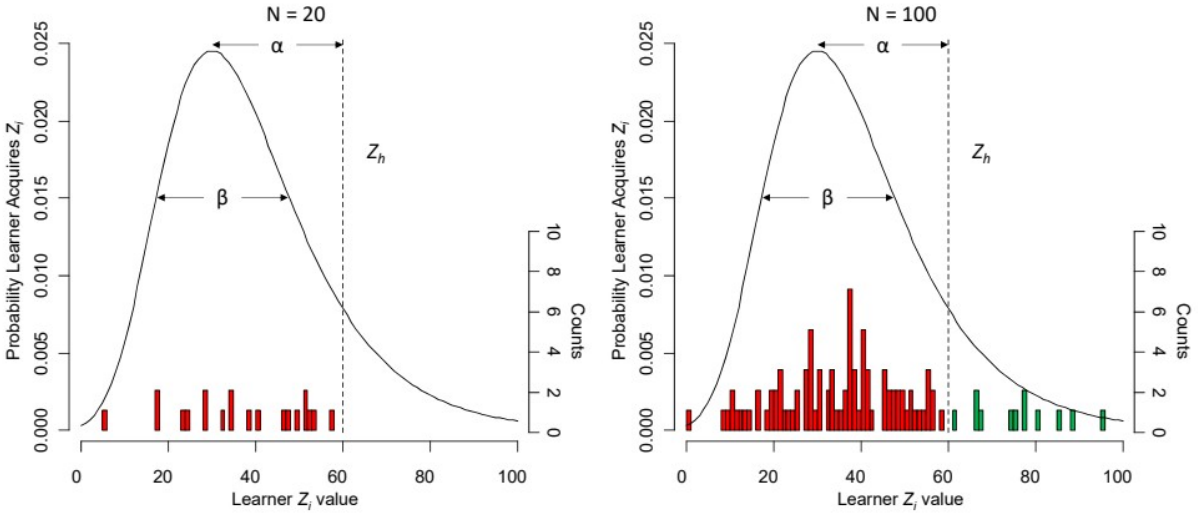


Figure 1: **Gumbel distribution from Henrich’s Tasmanian model**

The distributions depict the probability of a learner *i* acquiring different values of skill, *z* (z_i), for two different population sizes *N*. The vertical dotted line shows the z value of the highest-skilled demonstrator being copied (z_h). Learning error, determined by *α*, reduces the likelihood of z_h being reached. Inferences, experiments and luck, determined by β, increase the chances of the learner improving on z_h (the area under the curve to the right of the dotted line). Vertical bars show N random

draws from each distribution, representing N learners' z_i values. Red bars represent inferior z_i relative to z_h, green bars represent superior z_i relative to z_h. On the left, a small population (N=20) results in a population-level decline in skill, as no learner matches or exceeds z_h. On the right, a large population (N=100) features some learners who exceed z_h, resulting in an improvement in the next generation.

Box 2: Linking models and data in the lab

Experimental approaches are useful for investigating the relationship between demography and CCE because essential elements of theoretical models can be implemented under tightly controlled conditions, and tested against actual human behaviour (rather than modellers' assumptions about human behaviour) [111, 112].

As noted in the main text, the majority of experimental studies have found support for the general predictions of demographic models [27-31]. This is all the more surprising given that these studies are remarkably diverse in experimental tasks, group sizes and inter-individual interactions. Yet, it is worth highlighting that most experimental designs significantly deviate from the models they claim to test. In the main text we discuss one example, where experiments offer social learners the opportunity to combine information from multiple cultural demonstrators [29-31], rather than learn from a single successful demonstrator as in the most-cited demographic models (see Box 1). The role of recombination across existing cultural traits has been stressed by scholars from multiple fields [113-115], and increased opportunities for recombination certainly is one pathway by which effective population size might affect CCE [101]. Yet, most experiments are presented as tests of models that do not feature recombination between existing traits and in which effective population size mostly affects CCE by buffering the risk of losing cultural information (see Box 1). Still other experiments have relied on tasks in which cultural loss is unlikely to occur [31]. Thus, even though these experiments support the population size hypothesis, it is not always clear whether they provide appropriate tests of the theoretical models which they cite.

Maybe more problematic are experiments where results showing no relationship between demography and CCE are used to question the validity of theoretical models despite featuring different assumptions to those models. A recent experiment, for instance, had chains of participants make and throw paper airplanes, with each participant able to learn from 1, 2 or 4 previous participants [33]. Apparently contrary to the demographic hypothesis, flight distance only increased in the 1-demonstrator condition, not the 2- and 4-demonstrator conditions. Yet this experimental design prevented participants from learning from the demonstrator of their choice. Instead participants were forced to attend to multiple, randomly ordered demonstrators for 1.5 minutes each. Yet, Henrich's model explicitly holds that it is the combination of the amount of beneficial cultural information (which increases in larger groups) and the selective choices of cultural learners that promotes CCE. Fay et al.'s results are consistent with the former in showing that larger groups produce greater variation in distance flight and give participants access to more efficient planes. But the constraints imposed on social learning strategies inhibited CCE in large groups by making learning more difficult in those groups.

Discrepancies between experiments and models are not *inherently* a problem: the assumptions of models can always be challenged and mechanisms other than those considered in theoretical models are worth investigating. Yet, the experimental literature would benefit from being more explicit about the theoretical basis underpinning the specifics of experimental designs and how they relate to theoretical models.

545

Box 3: Linking models and data in the wild

Several studies have investigated whether there exists a correlation between toolkit size or composition and population size in natural populations [13, 14, 34-39], but there remain serious challenges in testing demographic effects on CCE in real world data.

One difficulty concerns limitations in what can be measured [58]. Henrich's model (see Box 1) describes the level of skill of an individual within a population, a variable that in an archaeological context can be interpreted as the number of tools or tool components attributable to an individual. Yet, archaeological studies typically only have access to population-level rather than individual-level data. This makes purported tests that use population-level assemblage measures largely irrelevant to Henrich's predictions [58]. Even though a recent model incorporating the appropriate population-level variable *does* predict a positive relationship between population size and toolkit size [58], these discrepancies illustrate the need to use appropriate measures when attempting to test a model and/or to adapt models so they can properly be tested using empirical data.

A second difficulty is that demography has multiple aspects that can be difficult to fully take into account in ethnographic and archaeological studies. In the main text we discuss one example of this, where empirical data regarding census population sizes are used to test (and purportedly fail to support) the Tasmanian model without taking contact rates into account. Furthermore, recent models suggest that historical variations in population size and connectedness are as important as immediate demographic contexts in determining cultural complexity in

569 a population [58, 64, 68]. Some models, for instance, show that the number of traits
570 in a population should depend not only on the current population size but also on
571 the history of population growth and decline [58, 64]. This can blur the relationship
572 between population size and CCE because growing populations can have fewer
573 cultural traits than smaller, declining populations. Similarly, two populations of the
574 same size might be associated with toolkits of different sizes due to different
575 demographic trajectories. Models also suggest that changes in interconnectedness
576 can result in different outcomes including transient increases in cultural complexity
577 [68]. The effects of population histories represent a challenge for archaeologists
578 whose data represent a record of aggregated events spanning long periods of time
579 during which both population size and interconnectedness might have varied.
580 Further models are needed to determine what testable signatures these dynamics
581 might have left in the past for archaeologists and historians to detect.

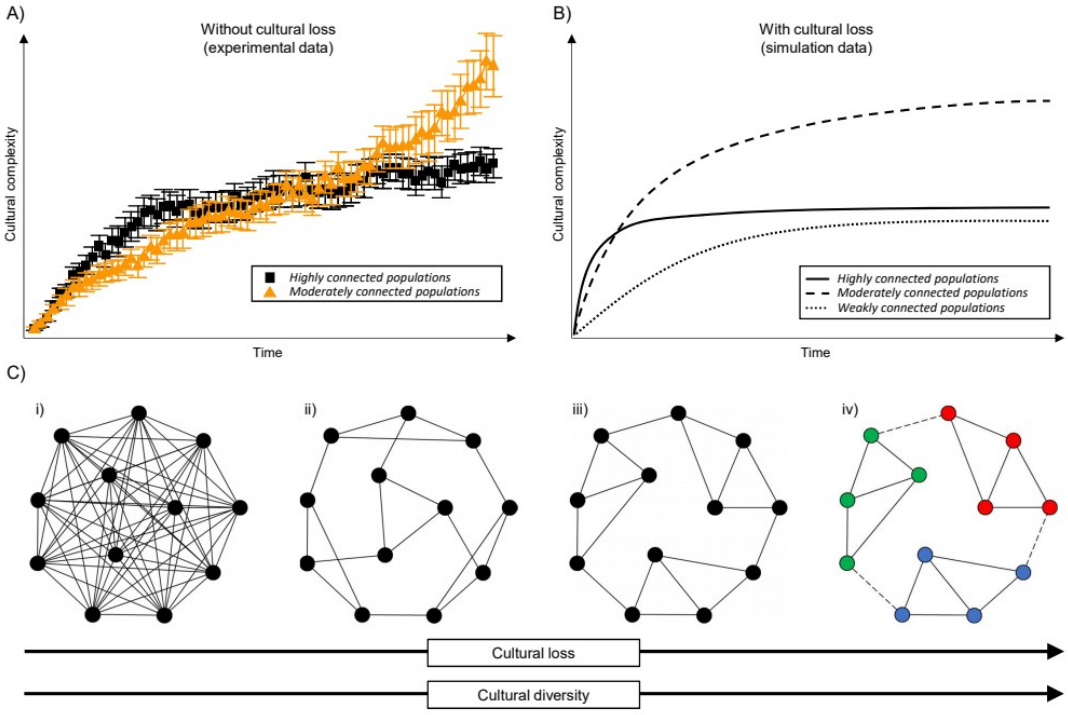
582 Finally, demographic factors determine an upper boundary to the level of
583 cultural complexity that can be reached by a population, but do not entirely
584 determine the actual level reached by a population. Assuming that increased cultural
585 complexity is beneficial, increases in population size should result in increases in
586 cultural complexity but only because this relaxes constraints on CCE. A full
587 understanding of CCE in natural populations requires both drivers of CCE and
588 constraints to be taken into account. To that end, more research is needed to
589 identify the factors that combine with demography to determine CCE in natural
590 populations, such as environmental harshness [54] and instability [116] or
591 accumulated cultural traits themselves [61, 117, 118].

Box 4: Is human multilevel social structure beneficial to CCE?

Recent theoretical and experimental studies have challenged the assumption that anything that maximizes the flow of cultural information should positively impact innovation rates (Figure 2A-B). These results have led scholars to wonder whether CCE in human populations has benefited from our unique multilevel social structure via the partial constraints it imposes on information flow [67]. A recent simulation study provided support for this by showing that real hunter-gatherers' social networks allow the coexistence of multiple cultural lineages, thus promoting the emergence of innovations [90].

However, while characterizing actual networks is useful for understanding how cultural information is expected to spread, many (still largely unknown) parameters need to be taken into account before establishing whether, and if so why, human multilevel social structure promotes CCE. Previous work has shown, for instance, that the effect of network structure on CCE is mediated by factors such as individuals' probabilities of innovating (because even strong constraints on information flow prevent cultural diversification if innovation rates are low [69]) and the extent to which innovation depends on cultural diversity (because constraints on information flow both slow down and limit CCE when innovation does not depend on recombination [69]). In the aforementioned simulation study [90], both individuals' opportunity to innovate, and possibilities for recombination, were determined by the properties of an artificial cultural fitness that was designed to permit innovation through incremental improvement and recombination [67], but whose relevance to rates of CCE in natural populations is uncertain.

615 Maybe more importantly, the effect of network structure on cultural *loss* was
616 not considered in those simulations [90]. When cultural loss is not taken into
617 account, constraints on information flow necessarily benefit CCE by promoting
618 cultural diversification. In more realistic situations, constraints on information flow
619 expose populations to higher rates of cultural loss, which can prevent cultural
620 diversification [119]. Moreover, even if they have diverse cultural repertoires,
621 sparsely connected populations can be unlikely to reach high levels of cultural
622 complexity because of their inability to maintain complex cultural traits [69]. Thus,
623 given our current limited knowledge about rates of loss and innovation, and
624 opportunities for recombination, in real-world populations, it is not clear whether the
625 network structure documented in [90] positively affects CCE or whether cultural
626 complexity in hunter-gatherer populations would benefit from more connectedness
627 by being less susceptible to cultural loss. Answering this question will require an
628 evaluation of how sparse networks made of strong ties (e.g. kin and friendship ties)
629 balance cultural loss and cultural diversity (Figure 2C).



631 **Figure 2: Trading cultural loss and diversity in structured populations.** (A)
632 Experimental results show that moderately connected populations are slower at
633 accumulating innovations but eventually reach higher levels of cultural complexity
634 than highly connected populations when innovation depends on cultural diversity.
635 Adapted from [67]. (B) Simulation models show that optimal rates of accumulation
636 are reached for intermediate levels of connectedness when populations are exposed
637 to cultural loss. Relative rates of accumulation between variously connected
638 populations depend on parameters such as rates of innovation and cultural loss,
639 and the extent to which innovation depends on cultural diversity (not shown).
640 Adapted from [69]. (C) Patterns of connectedness affect both cultural loss and
641 diversity. (i) In fully connected networks made of permanent links (solid lines), the

642 average number of steps required to connect any two individuals (i.e. path length) is
643 minimal and the efficiency with which information spreads is maximal. This reduces
644 the risks of cultural but decreases cultural diversity. (ii) Removing ties increases the
645 average path length between individuals and results in less efficient networks (e.g.
646 from i to ii). (iii) Networks composed of individuals tied to the same number of
647 neighbors can also vary in efficiency due to differences in average clustering
648 coefficients (a measure that reflects the “cliquishness” of a network [120]).
649 Increasing the average clustering coefficient results in less efficient networks (e.g.
650 from ii to iii). (iv) Intermittent links between different parts of a network (dotted lines)
651 further constrain information flow and result in substructures that are more likely to
652 culturally diverge by isolation (illustrated by different colors) but also more likely to
653 suffer from cultural loss.

Glossary

Demography: the size and structure of a population of individuals within which CCE occurs

Cumulative cultural evolution (CCE): the repeated modification and social learning of behavioural traits from individual to individual and over successive generations, such that the cultural traits improve in some desired measure of efficiency (typically a proxy for fitness)

Innovation: the generation of novel cultural variation, either via refinement or recombination

Refinement: improving an existing cultural trait, typically through a small, gradual change

Recombination: the bringing together of existing cultural traits to form a new functional trait

Tasmanian model: an influential early model of how population size constrains CCE (see Box 1)

Cultural drift: cultural change due to random sampling error, which is heavily dependent on population size and structure (see Box 1)

Structural barriers: blocks on information flow due to the structure of the population, e.g. individuals simply not coming into contact with one another

Behavioural barriers: blocks on information flow due to behavioural tendencies such as an unwillingness to teach hard-to-learn skills, despite contact

Effective population structure: the structure, resulting from the combined effects of structural and behavioral barriers, that constraints the flow of cultural information

Demonstrator: an individual who serves as a source of social information

Acknowledgments

We thank four reviewers and Rob Boyd for valuable comments on the manuscript. MD thanks Alex Alvergne, Slimane Dridi and Vivek Venkataraman for helpful discussions. This work was supported by the French Agence Nationale de la Recherche (under the Investissement d'Avenir programme ANR 17-EURE-0010) and the European Union's Horizon 2020 research and innovation programme (under Marie Sklodowska-Curie grant agreement number 748310).

References

1. Richerson, P.J. and Boyd, R. (2005) Not by genes alone, University of Chicago Press.

2. Henrich, J. (2015) The secret of our success: how culture is driving human evolution, domesticating our species, and making us smarter, Princeton University Press.

3. Boyd, R. et al. (2011) The cultural niche: Why social learning is essential for human adaptation. Proceedings of the National Academy of Sciences of the United States of America 108, 10918-10925.

4. Boyd, R. et al. (2013) The cultural evolution of technology: facts and theories. Cultural evolution: society, technology, language, and religion, 119-142.

5. Mesoudi, A. and Thornton, A. (2018) What is cumulative cultural evolution? Proceedings of the Royal Society B: Biological Sciences 285 (1880), 20180712.

6. Derex, M. et al. (2019) Causal understanding is not necessary for the improvement of culturally evolving technology. Nature Human Behaviour 3 (5), 446-452.

7. Muthukrishna, M. and Henrich, J. (2016) Innovation in the collective brain. Philosophical Transactions of the Royal Society of London B: Biological Sciences 371 (1690).

8. Cavalli-Sforza, L.L. and Feldman, M.W. (1981) Cultural transmission and evolution: A quantitative approach, Princeton University Press.

9. Boyd, R. and Richerson, P.J. (1985) Culture and the evolutionary process, University of Chicago Press.

10. Mesoudi, A. (2011) Cultural Evolution: How Darwinian Theory Can Explain

720 Human Culture and Synthesize the Social Sciences, University of Chicago Press.
721 11. Henrich, J. (2004) Demography and cultural evolution: How adaptive cultural
722 processes can produce maladaptive losses - The Tasmanian case. American
723 Antiquity 69 (2), 197-214.
724 12. Eerkens, J.W. and Lipo, C.P. (2007) Cultural Transmission Theory and the
725 Archaeological Record: Providing Context to Understanding Variation and Temporal
726 Changes in Material Culture. Journal of Archaeological Research 15 (3), 239-274.
727 13. Powell, A. et al. (2009) Late Pleistocene Demography and the Appearance of
728 Modern Human Behavior. Science 324 (5932), 1298-1301.
729 14. Marquet, P.A. et al. (2012) Emergence of social complexity among coastal
730 hunter-gatherers in the Atacama Desert of northern Chile. Proceedings of the
731 National Academy of Sciences 109 (37), 14754-14760.
732 15. French, J.C. (2016) Demography and the Palaeolithic Archaeological Record.
733 Journal of Archaeological Method and Theory 23 (1), 150-199.
734 16. Mackay, A. et al. (2014) Coalescence and fragmentation in the late Pleistocene
735 archaeology of southernmost Africa. Journal of Human Evolution 72, 26-51.
736 17. Greenbaum, G. et al. (2019) Was inter-population connectivity of Neanderthals
737 and modern humans the driver of the Upper Paleolithic transition rather than its
738 product? Quaternary Science Reviews 217, 316-329.
739 18. Kuhn, S.L. (2012) Emergent Patterns of Creativity and Innovation in Early
740 Technologies. In Developments in Quaternary Sciences (Elias, S. ed), pp. 69-87,
741 Elsevier.
742 19. Riede, F. (2009) The loss and re-introduction of bow-and-arrow technology: a

743 case study from the Northern European Late Paleolithic. Lithic Technology 34 (1),
744 27-45.
745 20. Jones, R. (1973) Emerging Picture of Pleistocene Australians. Nature 246 (5431),
746 278-281.
747 21. Cavalli-Sforza, L. and Feldman, M.W. (1973) Models for cultural inheritance I.
748 Group mean and within group variation. Theoretical Population Biology 4 (1), 42-55.
749 22. Neiman, F.D. (1995) Stylistic Variation in Evolutionary Perspective: Inferences
750 from Decorative Diversity and Interassemblage Distance in Illinois Woodland
751 Ceramic Assemblages. American Antiquity 60 (1), 7-36.
752 23. Shennan, S. (2001) Demography and Cultural Innovation: a Model and its
753 Implications for the Emergence of Modern Human Culture. Cambridge
754 Archaeological Journal 11 (01), 5-16.
755 24. Tomasello, M. et al. (1993) Cultural Learning. Behavioral and Brain Sciences 16
756 (3), 495-511.
757 25. Tennie, C. et al. (2009) Ratcheting up the ratchet: on the evolution of cumulative
758 culture. Philosophical Transactions of the Royal Society B-Biological Sciences 364
759 (1528), 2405-2415.
760 26. Lewis, H.M. and Laland, K.N. (2012) Transmission fidelity is the key to the build-
761 up of cumulative culture. Philosophical Transactions of the Royal Society B-
762 Biological Sciences 367 (1599), 2171-2180.
763 27. Derex, M. et al. (2013) Experimental evidence for the influence of group size on
764 cultural complexity. Nature 503, 389-391.
765 28. Wisdom, T.N. et al. (2013) Social Learning Strategies in Networked Groups.

766 Cognitive Science 37 (8), 1383-1425.
767 29. Muthukrishna, M. et al. (2014) Sociality influences cultural complexity.
768 Proceedings of the Royal Society B: Biological Sciences 281 (1774), 20132511.
769 30. Kempe, M. and Mesoudi, A. (2014) An experimental demonstration of the effect
770 of group size on cultural accumulation. Evolution and Human Behavior 35 (4), 285-
771 290.
772 31. Derex, M. and Boyd, R. (2015) The foundations of the human cultural niche. Nat
773 Commun 6, 8398.
774 32. Caldwell, C.A. and Millen, A.E. (2010) Human cumulative culture in the
775 laboratory: Effects of (micro) population size. Learning & Behavior 38 (3), 310-318.
776 33. Fay, N. et al. (2019) Increasing population size can inhibit cumulative cultural
777 evolution. Proceedings of the National Academy of Sciences, 201811413.
778 34. Kline, M.A. and Boyd, R. (2010) Population size predicts technological
779 complexity in Oceania. Proceedings of the Royal Society B-Biological Sciences 277
780 (1693), 2559-2564.
781 35. Collard, M. et al. (2013) Population Size and Cultural Evolution in Nonindustrial
782 Food-Producing Societies. PLOS ONE 8 (9), e72628.
783 36. Collard, M. et al. (2005) Causes of Toolkit Variation Among Hunter-Gatherers: A
784 Test of Four Competing Hypotheses. Canadian Journal of Archaeology / Journal
785 Canadien d'Archéologie 29 (1), 1-19.
786 37. Collard, M. et al. (2013) Risk, mobility or population size? Drivers of
787 technological richness among contact-period western North American
788 hunterâ€“gatherers. Philosophical Transactions of the Royal Society B: Biological

789 Sciences 368 (1630).
790 38. Collard, M. et al. (2013) Population Size as an Explanation for Patterns in the
791 Paleolithic Archaeological Record: More Caution Is Needed. Current Anthropology
792 54 (S8), S388-S396.
793 39. Buchanan, B. et al. (2015) Drivers of technological richness in prehistoric Texas:
794 an archaeological test of the population size and environmental risk hypotheses.
795 Archaeological and Anthropological Sciences, 1-10.
796 40. Henrich, J. et al. (2016) Understanding cumulative cultural evolution.
797 Proceedings of the National Academy of Sciences 113 (44), E6724-E6725.
798 41. Acerbi, A. et al. (2017) Cultural complexity and demography: The case of
799 folktales. Evolution and Human Behavior 38 (4), 474-480.
800 42. Arthur, W.B. (2009) The nature of technology: What it is and how it evolves,
801 Simon and Schuster.
802 43. Nettle, D. (1995) Segmental inventory size, word length, and communicative
803 efficiency. Linguistics 33 (2), 359-367.
804 44. Hay, J. and Bauer, L. (2007) Phoneme Inventory Size and Population Size.
805 Language 83 (2), 388-400.
806 45. Moran, S. et al. (2012) Revisiting population size vs. phoneme inventory size.
807 Language, 877-893.
808 46. Wichmann, S. et al. (2011) Phonological diversity, word length, and population
809 sizes across languages: The ASJP evidence. 15 (2), 177.
810 47. Wichmann, S. and Holman, E.W. (2009) Population Size and Rates of Language
811 Change. Human Biology 81 (3), 259-274, 16.

48. Bromham, L. et al. (2015) Rate of language evolution is affected by population size. Proceedings of the National Academy of Sciences.

49. Greenhill, S.J. et al. (2018) Population Size and the Rate of Language Evolution: A Test Across Indo-European, Austronesian, and Bantu Languages. Frontiers in Psychology 9 (576).

50. Kirby, S. et al. (2008) Cumulative cultural evolution in the laboratory: An experimental approach to the origins of structure in human language. Proceedings of the National Academy of Sciences of the United States of America 105 (31), 10681-10686.

51. McElreath, R. et al. (2003) Shared norms and the evolution of ethnic markers. Current Anthropology 44 (1), 122-129.

52. Rogers, D.S. and Ehrlich, P.R. (2008) Natural selection and cultural rates of change. Proceedings of the National Academy of Sciences of the United States of America 105 (9), 3416-3420.

53. Vaesen, K. et al. (2016) Population size does not explain past changes in cultural complexity. Proceedings of the National Academy of Sciences 113 (16), E2241-E2247.

54. Torrence, R. (1989) Re-tooling: towards a behavioral theory of stone tools. Time, energy and stone tools, 57-66.

55. Collard, M. et al. (2011) What drives the evolution of hunter-gatherer subsistence technology? A reanalysis of the risk hypothesis with data from the Pacific Northwest. Philosophical Transactions of the Royal Society B: Biological Sciences 366 (1567), 1129-1138.

56. Grove, M. (2018) Hunter-gatherers adjust mobility to maintain contact under climatic variation. Journal of Archaeological Science: Reports 19, 588-595.

57. Kobayashi, Y. and Aoki, K. (2012) Innovativeness, population size and cumulative cultural evolution. Theoretical Population Biology 82 (1), 38-47.

58. Aoki, K. (2018) On the absence of a correlation between population size and 'toolkit size' in ethnographic hunter-gatherers. Philosophical Transactions of the Royal Society B: Biological Sciences 373 (1743), 20170061.

59. Lehmann, L. et al. (2011) On the number of independent cultural traits carried by individuals and populations. Philosophical Transactions of the Royal Society B: Biological Sciences 366 (1563), 424-435.

60. Vaesen, K. (2012) Cumulative Cultural Evolution and Demography. Plos One 7 (7).

61. Mesoudi, A. (2011) Variable Cultural Acquisition Costs Constrain Cumulative Cultural Evolution. Plos One 6 (3), e18239.

62. Kolodny, O. et al. (2015) Evolution in leaps: The punctuated accumulation and loss of cultural innovations. Proceedings of the National Academy of Sciences 112 (49), E6762-E6769.

63. Fogarty, L. and Creanza, N. (2017) The niche construction of cultural complexity: interactions between innovations, population size and the environment. Philosophical Transactions of the Royal Society B: Biological Sciences 372 (1735), 20160428.

64. Fogarty, L. et al. (2017) The Driving Forces of Cultural Complexity. Human Nature 28 (1), 39-52.

858 65. Aoki, K. (2019) Cultural bistability and connectedness in a subdivided
859 population. Theoretical Population Biology.
860 66. Bentley, R.A. and O'brien, M.J. (2011) The selectivity of social learning and the
861 tempo of cultural evolution. Journal of Evolutionary Psychology 9 (2), 125-141.
862 67. Derex, M. and Boyd, R. (2016) Partial connectivity increases cultural
863 accumulation within groups. Proceedings of the National Academy of Sciences 113
864 (11), 2982-2987.
865 68. Creanza, N. et al. (2017) Greater than the sum of its parts? Modelling population
866 contact and interaction of cultural repertoires. Journal of The Royal Society Interface
867 14 (130).
868 69. Derex, M. et al. (2018) Divide and conquer: intermediate levels of population
869 fragmentation maximize cultural accumulation. Philosophical Transactions of the
870 Royal Society B: Biological Sciences 373 (1743), 20170062.
871 70. Lazer, D. and Friedman, A. (2007) The Network Structure of Exploration and
872 Exploitation. Administrative Science Quarterly 52 (4), 667-694.
873 71. Fang, C. et al. (2009) Balancing Exploration and Exploitation Through Structural
874 Design: The Isolation of Subgroups and Organizational Learning. Organization
875 Science 21 (3), 625-642.
876 72. Mason, W.A. et al. (2008) Propagation of innovations in networked groups.
877 Journal of Experimental Psychology: General 137 (3), 422-433.
878 73. Mason, W. and Watts, D.J. (2012) Collaborative learning in networks.
879 Proceedings of the National Academy of Sciences 109 (3), 764-769.
880 74. Barkoczi, D. and Galesic, M. (2016) Social learning strategies modify the effect

881 of network structure on group performance. Nature Communications 7 (1), 13109.
882 75. Burt, R.S. (2004) Structural Holes and Good Ideas. American Journal of
883 Sociology 110 (2), 349-399.
884 76. Flynn, E. and Whiten, A. (2010) Studying children's social learning experimentally
885 "in the wild". Learning & Behavior 38 (3), 284-296.
886 77. Centola, D. and Macy, M. (2007) Complex Contagions and the Weakness of
887 Long Ties. American Journal of Sociology 113 (3), 702-734.
888 78. Carja, O. and Creanza, N. (2019) The evolutionary advantage of cultural memory
889 on heterogeneous contact networks. Theoretical Population Biology 129, 118-125.
890 79. Malinsky-Buller, A. and Hovers, E. (2019) One size does not fit all: Group size
891 and the late middle Pleistocene prehistoric archive. Journal of Human Evolution 127,
892 118-132.
893 80. Mazet, O. et al. (2016) On the importance of being structured: instantaneous
894 coalescence rates and human evolution—lessons for ancestral population size
895 inference? Heredity 116 (4), 362-371.
896 81. Kovacevic, M. et al. (2015) Simulating Geographical Variation in Material Culture:
897 Were Early Modern Humans in Europe Ethnically Structured? In Learning Strategies
898 and Cultural Evolution during the Palaeolithic (Mesoudi, A. and Aoki, K. eds), pp.
899 103-120, Springer Japan.
900 82. Mills, B.J. (2017) Social Network Analysis in Archaeology. Annual Review of
901 Anthropology 46 (1), 379-397.
902 83. Peeples, M.A. (2019) Finding a Place for Networks in Archaeology. Journal of
903 Archaeological Research 27 (4), 451-499.

904 84. Romano, V. et al. (2020) A multilevel analytical framework for studying cultural
905 evolution in prehistoric hunter–gatherer societies. Biological Reviews n/a (n/a).
906 85. Chapais, B. (2013) Monogamy, strongly bonded groups, and the evolution of
907 human social structure. Evolutionary Anthropology: Issues, News, and Reviews 22
908 (2), 52-65.
909 86. Hill, K.R. et al. (2011) Co-Residence Patterns in Hunter-Gatherer Societies Show
910 Unique Human Social Structure. Science 331 (6022), 1286-1289.
911 87. Hill, K.R. et al. (2014) Hunter-Gatherer Inter-Band Interaction Rates: Implications
912 for Cumulative Culture. PLoS ONE 9 (7), e102806.
913 88. Bird, D.W. et al. (2019) Variability in the organization and size of hunter-gatherer
914 groups: Foragers do not live in small-scale societies. Journal of Human Evolution
915 131, 96-108.
916 89. Migliano, A.B. et al. (2017) Characterization of hunter-gatherer networks and
917 implications for cumulative culture. Nature Human Behaviour 1 (2), 0043.
918 90. Migliano, A.B. et al. (2020) Hunter-gatherer multilevel sociality accelerates
919 cumulative cultural evolution. Science Advances 6 (9), eaax5913.
920 91. Salali, Gul D. et al. (2016) Knowledge-Sharing Networks in Hunter-Gatherers and
921 the Evolution of Cumulative Culture. Current Biology 26 (18), 2516-2521.
922 92. Durham, W.H. (1992) Applications of Evolutionary Culture Theory. Annual Review
923 of Anthropology 21, 331-355.
924 93. Tehrani, J.J. and Collard, M. (2013) Do Transmission Isolating Mechanisms
925 (TRIMS) Influence Cultural Evolution?, Berghahn.
926 94. Apicella, C.L. et al. (2012) Social networks and cooperation in hunter-gatherers.

927 Nature 481 (7382), 497-U109.
928 95. Centola, D. et al. (2007) Homophily, cultural drift, and the co-evolution of cultural
929 groups. Journal of Conflict Resolution 51 (6), 905-929.
930 96. Kandler, A. and Caccioli, F. (2016) Networks, homophily, and the spread of
931 innovations. In The connected past: Challenges to network studies in archaeology
932 and history, pp. 175-198, Oxford Univ. Press.
933 97. Smolla, M. and Akçay, E. (2019) Cultural selection shapes network structure.
934 Science Advances 5 (8), eaaw0609.
935 98. Henrich, J. and Gil-White, F.J. (2001) The evolution of prestige - Freely conferred
936 deference as a mechanism for enhancing the benefits of cultural transmission.
937 Evolution and Human Behavior 22 (3), 165-196.
938 99. Mesoudi, A. (2008) An experimental simulation of the "copy-successful-
939 individuals" cultural learning strategy: adaptive landscapes, producer-scrounger
940 dynamics, and informational access costs. Evolution and Human Behavior 29 (5),
941 350-363.
942 100. Derex, M. et al. (2014) How does competition affect the transmission of
943 information? Evolution and Human Behavior 35 (2), 89-95.
944 101. Henrich, J. (2009) The Evolution of Innovation-Enhancing Institutions. In
945 Innovation in Cultural Systems: Contributions in Evolution Anthropology (Shennan,
946 S.J. and O'Brien, M.J. eds), MIT.
947 102. Wiessner, P. (1981) Hxaro: A Regional System of Reciprocity for Reducing Risk
948 Among the !Kung San, University of Michigan.
949 103. Wiessner, P. (1997) Seeking guidelines through an evolutionary approach: style

950 revisited among the! Kung San (Ju/'hoansi) of the 1990s. Archeological Papers of
951 the American Anthropological Association 7 (1), 157-176.
952 104. Machin, A. and Dunbar, R. (2016) Is Kinship a Schema? Moral Decisions and
953 the Function of the Human Kin Naming System. Adaptive Human Behavior and
954 Physiology 2 (3), 195-219.
955 105. Langergraber, K.E. et al. (2007) The limited impact of kinship on cooperation in
956 wild chimpanzees. Proceedings of the National Academy of Sciences 104 (19),
957 7786-7790.
958 106. Lewis, H.M. et al. (2014) High mobility explains demand sharing and enforced
959 cooperation in egalitarian hunter-gatherers. Nature Communications 5 (1), 5789.
960 107. Macfarlan, S.J. et al. (2014) Lethal coalitionary aggression and long-term
961 alliance formation among Yanomamö men. Proceedings of the National Academy of
962 Sciences 111 (47), 16662-16669.
963 108. Bentley, R.A. et al. (2004) Random drift and culture change. Proceedings of the
964 Royal Society of London. Series B: Biological Sciences 271 (1547), 1443-1450.
965 109. Bell, A.V. (2015) Linking Observed Learning Patterns to the Evolution of Cultural
966 Complexity. Current Anthropology 56 (2), 277-281.
967 110. Andersson, C. and Read, D. (2016) The Evolution of Cultural Complexity: Not
968 by the Treadmill Alone. Current Anthropology 57 (3), 261-286.
969 111. Mesoudi, A. (2007) Using the methods of experimental social psychology to
970 study cultural evolution. Journal of Social, Evolutionary, and Cultural Psychology 1
971 (2), 35-58.
972 112. Mesoudi, A. and Whiten, A. (2008) The multiple roles of cultural transmission

973 experiments in understanding human cultural evolution. Philosophical Transactions
974 of the Royal Society B-Biological Sciences 363 (1509), 3489-3501.
975 113. Enquist, M. et al. (2011) Modelling the evolution and diversity of cumulative
976 culture. Philosophical Transactions of the Royal Society B-Biological Sciences 366
977 (1563), 412-423.
978 114. Basalla, G. (1988) The evolution of technology, UK: Cambridge University
979 Press.
980 115. Fleming, L. (2001) Recombinant Uncertainty in Technological Search.
981 Management Science 47 (1), 117-132.
982 116. Fogarty, L. (2018) Cultural complexity and evolution in fluctuating environments.
983 Philosophical Transactions of the Royal Society B: Biological Sciences 373 (1743),
984 20170063.
985 117. Enquist, M. et al. (2008) Why does human culture increase exponentially?
986 Theoretical Population Biology 74 (1), 46-55.
987 118. Kolodny, O. et al. (2016) Game-Changing Innovations: How Culture Can
988 Change the Parameters of Its Own Evolution and Induce Abrupt Cultural Shifts.
989 PLOS Computational Biology 12 (12), e1005302.
990 119. Premo, L.S. (2012) Local extinctions, connectedness, and cultural evolution in
991 structured populations. Advances in Complex Systems 15 (01n02), 1150002.
992 120. Watts, D.J. and Strogatz, S.H. (1998) Collective dynamics of ‘small-world’
993 networks. Nature 393 (6684), 440-442.
994